DECIDUOUS THICKET COMMUNITIES IN NORTHERN RHODESIA

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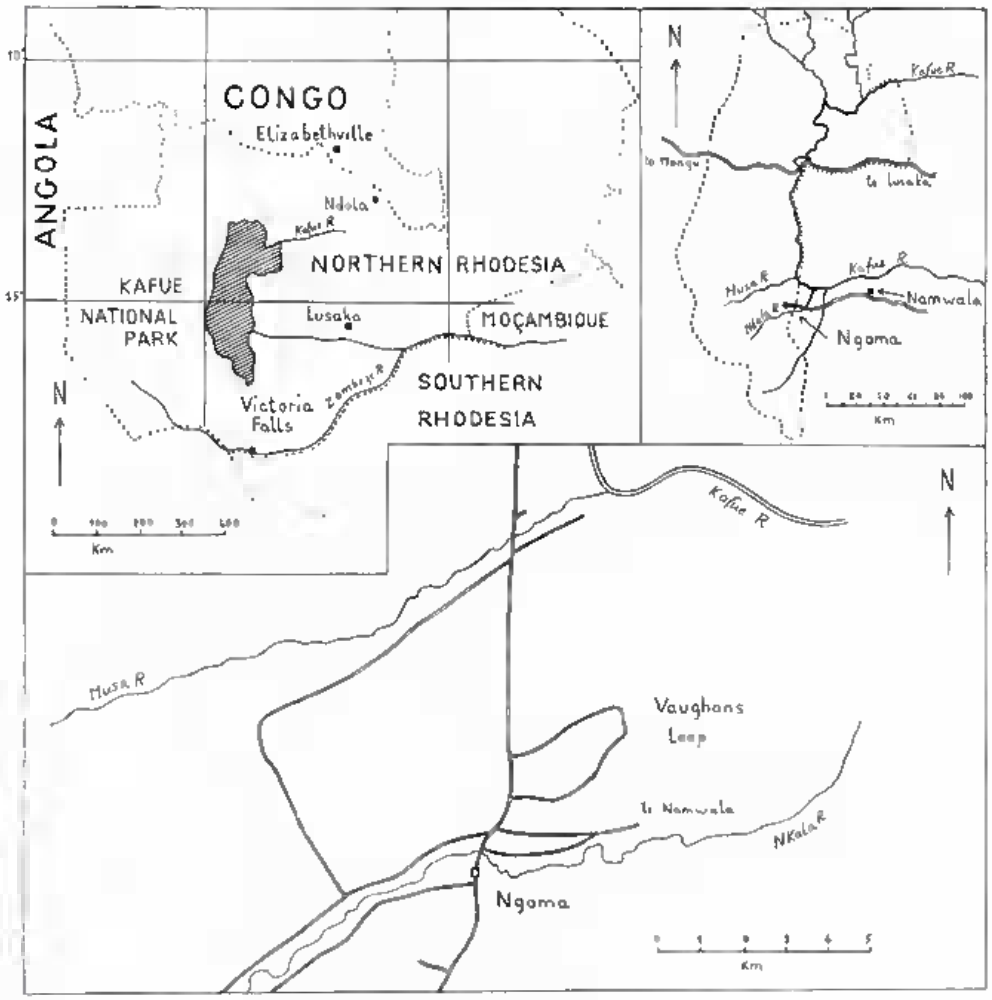
INTRODUCTION

In the Lowland Tropical Rain Forest regions of West and Equatorial Africa, the occurrence and appearance of thicket communities have been well described. Such communities, as has been shown by various workers including Aubréville (1949), Keay (1949), Richards (1952), Ross (1954), Lebrun et Gilbert (1954), and Taylor (1960), originate from the farming management practices of the indigenous population of the forest, which involve the abandoning for a time of cleared and cultivated land, to permit some degree of restoration of soil fertility under a varying period of forest regrowth; the method of so-called " shifting cultivation ". Such thicket communities formed in the tropical rain forest by the practice of shifting cultivation, are therefore seral stages in the regeneration of a climax vegetation somewhat approximating in structure, and floristic composition, to the original undisturbed forest cover.

However from the upland plateaux of Tropical Africa south of the Equator, once perhaps covered with uninterrupted woodlands and dry deciduous forests, thicket communities, whether seral or otherwise, have more rarely been described. In Northern Rhodesia reference to such vegetation is found in the work of Trapnell (1943), and Trapnell and Clothier (1937) who discuss and illustrate numerous thicket communities from various localities in Northern Rhodesia, but do not specifically define their ecological significance, or invariably relate them to other plant communities of this region.

The present investigation on a series of thicket communities in the Kafue National Park of Northern Rhodesia was begun in an endeavour to determine their ecological status, and the management practices which are a necessary prerequisite for preserving these important habitats, which are continously occupied by rhinoceros, grysbok, and several species of duiker, as well as used at particular seasons by buffalo, elephant and other game species.



DESCRIPTION OF THE AREA

The thickets investigated lie across the watershed between the Musa and Nkala, tributaries of the Kafue River (see map). Most of the area is covered by an aeolian deposit of Kalahari Sand of varying depth. The actual watershed is formed by a low ridge of Karroo Sandstone, which emerges above the deposit of Kalahari Sand. Closely surrounding the sandstone ridge are contact soils, intermediate in colour between the red sands of the ridge itself and the greyish white of the Kalahari Sand.

Climatic data for the area are supplied in Table I. Until as recently as 1957, African settlement continued in this area, although finally only on a minor scale, and the population practiced their traditional cultivation of maize and millet fields, the effect of which on the vegetation will later be described.

TABLE I

Meteorological data from Namwala, 15° 45' S, 26° 27' E.

Average annual rainfall

1921/1956 31.40 in.

Variation in annual rainfall

1951/52	41.0 in.	1956/57	20.8 in.
1952/53	37.0 in.	1957/58	46.9 in.
1953/54	34.3 in.	1958/59	35.0 in.
1954/55	34.2 in.	1959/60	27.5 in.
1955/56	27.4 in.	1960/61	40.0 in.

Average monthly rainfall 1921/1956

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
8.2	6.6	5.3	0.6	—	—	—	—	0.1	0.6	3.2	6.8

Temperature of coldest month — July

Maximum, Mean 77.9° F, Absolute 89° F.
Minimum, Mean 41.0° F, Absolute 28° F.

Temperature of hottest month — October

Maximum, Mean 93.5° F, Absolute 104° F.
Minimum, Mean 60.4° F, Absolute 45° F.

Relative Humidity of driest month (8 a.m.) — October : Monthly mean 50 %

Relative Humidity of wettest month (8 a.m.) — February : Monthly mean 88 %.

(All figures courtesy Federal Meteorological Department.)

The undisturbed, or at least, the uncultivated vegetation of the area has been described by TRAPNELL and CLOTHIER (1937) and is represented diagramatically in fig. 1. The deepest Kalahari Sands carry a cover of teak forest, which when unburnt has the structure of a dry deciduous forest (C.S.A., 1956), while the shallower soils thin out to *Isoberlinia — Brachystegia* woodlands; the mopane clays, without any cover of Kalahari Sand, carry discontinuous clumps of "Mopane Woodland" *(Colophospermum mopane)*. Depressions in the Kalahari Sand, often forming the upper sections of the drainage systems, are edaphic grasslands with no tree growth, known locally as "dambos".

In the area in question between the Musa and Nkala rivers, there are no mature teak trees, and no *Brachystegia* or *Julbernardia* species. The country in fact presents every sign of degradation under the effect of repeated late (September to October) grass fires. The sandstone ridge which forms the watershed still carries what can be described as Dry Dedicuous Forest, in which rather scattered groupings of mature trees of *Entandrophragma caudatum* some 20 to 25 m. high form emergents above a continuous canopy of small deciduous trees at a general level of approximately 7 to 10 m. Everywhere in this *Entandophragma* forest and in the adjoining thickets, game trails run through the vegetation,

between the coppicing tree clumps, making progress surprisingly easy. The animals responsible for maintaining the open nature of this thicket, according to the resident biologist of the Park, B. L. MITCHELL, are firstly buffalo, which browse in the thickets when grazing becomes scarce with the onset of the dry season, but before the leaves of this deciduous community are shed, and secondly elephants which seek out the ripe fruits of *Popowia obovata*, of which they are inordinately fond.

Coming off the crest of the sandstone ridge towards the Nkala river *Entandrophragma* forest soon disappears, but the understorey continues as thicket until it is in discontinuous contact, through a series of fire-holes, with a different thicket community containing many young teak trees, barely high enough yet to emerge above the thicket. From there this second thicket community gradually passes southwards into savanna woodland and on to the grassy floodplain of the Nkala River.

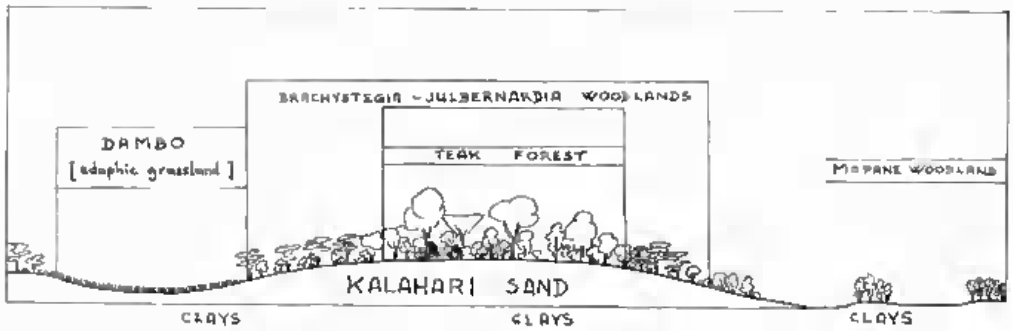


Fig. 1. — Hypothetical catena section through Kalahari Sand vegetation in the southern section of the Kafue National Park, illustrating the spatial relationships of Teak Forest, *Isoberlinia* — *Brachystegia* woodlands and Mopane Woodland.

Northwards the transition to savanna woodland is much more abrupt, although one small thicket is encountered astride the road less than a mile from the Musa river crossing. Either side of this main road north from Ngoma the thicket, with its *Entandrophragma* and teak variants, spreads out more or less along the sandstone ridge, intersected by many fire holes, which generally run in the direction of the prevailing S. wind and at an angle to the ridge.

Towards the south-western section of the area, that is on the contact soils south of the Karroo Sandstone ridge and approaching the great flood-plain of the Kafue River, a further thicket type is encountered, a thorny one dominated in places by *Dichrostachys cinerea*, in other places by *Acacia Fleckii*.

These four thicket communities, Karroo Sandstone thicket, Teak thicket, *Dichrostachys* thicket and *Acacia* thicket, seen from one of the several hills in the area, or from aerial photographs, all seem to intergrade to form a continuous but often dissected or interrupted thicket mass about 5 km. wide, running between the Musa and Nkala rivers.

It is the ecological status and inter-relationships of these several thicket communities which this present account attempts to elucidate.

A list of symbols used to indicate particular species on Karroo Sandstone soils is given in Table 2, and on Kalahari Sand in Table 3.

TABLE 2

Key to symbols used in illustrations of transects of vegetation on Karroo Sandstone soils.

As	*Acacia stenophylla*	Ee	*Euphorbia espinosa*
Bo	*Byrsocarpus orientalis*	Ft	*Fagara trigyna*
Ca	*Combretum apiculatum*	Gf	*Grewia flava*
Ce	*Combretum Engleri*	H	*Hippocratea africana*
Cg	*Cassipourea gummiflua*	Mf	*Maerua Friesii*
Cl	*Combretum elaeagnoides*	Rh	*Rhus sp.*
Cr	*Canthium Randii*	S	*Strychnos sp.*
Cs	*Combretum ghasalense*	Sw	*Strychnos* White no. 2
Dd	*Diplorhynchus condylocarpon*	Tm	*Terminalia mollis*
E	*Entandrophragma caudatum*	Vp	*Vitex payos*

TABLE 3

Key to symbols used in illustrations of transects of vegetation on Kalahari Sand.

Af	*Acacia Fleckii*	Dm	*Dalbergia Martinii.*
Ao	*Alchornia occidentalis*	Dn	*Dalbergiella nyassae.*
As	*Annona stenophylla.*	Ha	*Hymenocardia acida.*
B	*Baphia obovata.*	Mo	*Markhamia obtusiflora.*
Ba	*Burkea africana.*	Op	*Ochna pulchra.*
Bo	*Byrsocarpus orientalis.*	Os	*Ostryoderris Stuhlmannii.*
Bp	*Baikiaea plurijuga.*	Pa	*Pterocarpus angolensis.*
C	*Canthium sp.*	Pm	*Pseudolachnostylis maprouneifolia*
Ca	*Combretum apiculatum*	Rr	*Ricinodendron Rautenanii.*
Ca	*Citropsis daweana.*	Sa	*Steganotaenia araliacea.*
Cf	*Canthium franguta.*	Sl	*Securidaca longipedunculata.*
Cm	*Clerodendrum myricoides.*	Tb	*Terminalia brachystemma.*
Dc	*Dichrostachys cinerea.*	Tl	*Terminalia silozensis.*
Dd	*Diplorhynchus condylocarpon.*	Tm	*Terminalia mollis.*
Dl	*Diospyros lycioides.*	Vp	*Vitex payos.*

METHOD OF INVESTIGATION

Owing to the complexity of the vegetation patterns in this area, it was considered that the only completely objective method by which the several plant communities involved could be clearly demarcated

was by using an association technique such as described by HOPKINS (1957). This procedure is now being followed in a study proceeding in co-operation with Mr. B. L. MITCHELL; it will, however, be some considerable time before the results become available. Meanwhile it seemed worthwhile to attempt an analysis of the vegetation on a more subjective basis.

In this latter investigation which is the one described here, selected types of each plant community observed in the area were examined in detail, and a plan and profile diagram prepared of a typical portion. In some communities the area examined and described in this way was 20 feet (6.3 m.) square, but it ranged up to a rectangular plot 20 feet (6.3 m.) by 60 feet (19 m.). Generally speaking the thicket types proper contained too many plants for a larger area than the 20 feet (6.3 m.) square to be convenient for use; only the more open fire-devastated communities contained relatively few plants, and needed to be recorded over a longer transect area.

When all the basic types of plant community had been recognised, these were arranged in what appeared to be their seral relationships, with climax or undisturbed forest on the one hand, and on the other degraded vegetation arising from repeated burning alone, or from clearing for cultivation purposes followed by burning. The types of community recognised are described briefly and illustrated below.

DESCRIPTION OF PLANT COMMUNITIES RECOGNIZED

A. KARROO SANDSTONE SOILS

1. *Entandrophragma Forest.*

A profile and ground plan of this community are illustrated in fig. 2. It is found only towards the summit of the watershed ridge of Karroo sandstone, and from aerial photographs can be recognised as spreading along the ridge for a distance of 10 km. or so, with a width approaching two kilometres.

The forest floor is covered with leaf litter to a depth of 10-20 cm., and the network of animal trails between the clumps of understorey trees is somewhat sunken below the slight soil mounds surrounding these clumps. Lianes everywhere interlace the canopies of the understorey trees and the lower limbs of the larger *Entandrophragma* trees; *Hippocratea africana*, *Byrsocarpus africana*, *Dalbergia martini* and a species of *Strychnos* described by WHITE (1962) as "species 2" are the commonest liana species.

2. *Karroo Thicket.*

Moving south or north off the crest of the Karroo Sandstone Ridge, *Entandrophragma* disappears, but the understorey of the *Entandro-*

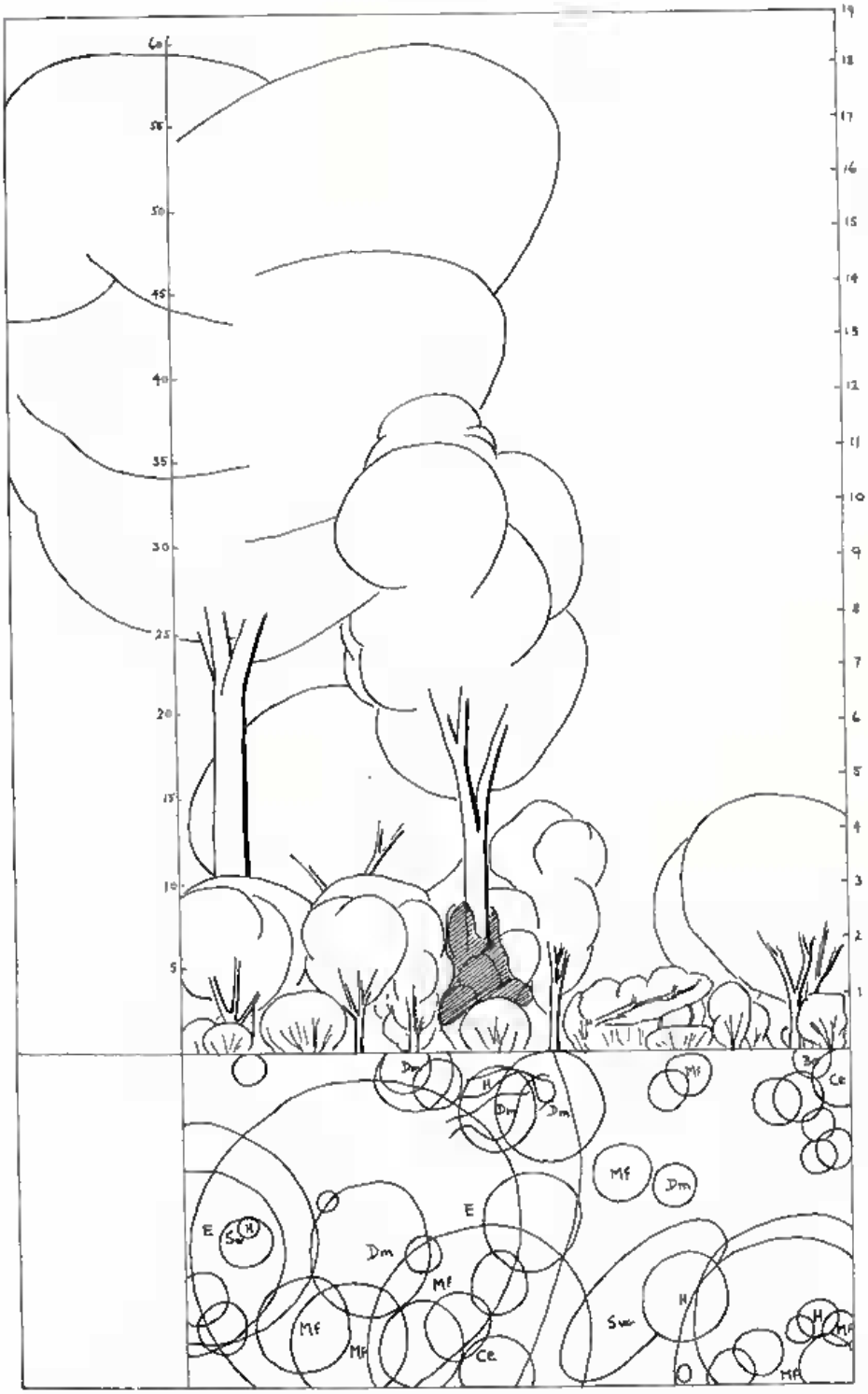


Fig. 2. — A profile diagram and ground plan of *Entandrophragma* Forest, some nine kilometres North of Ngoma.

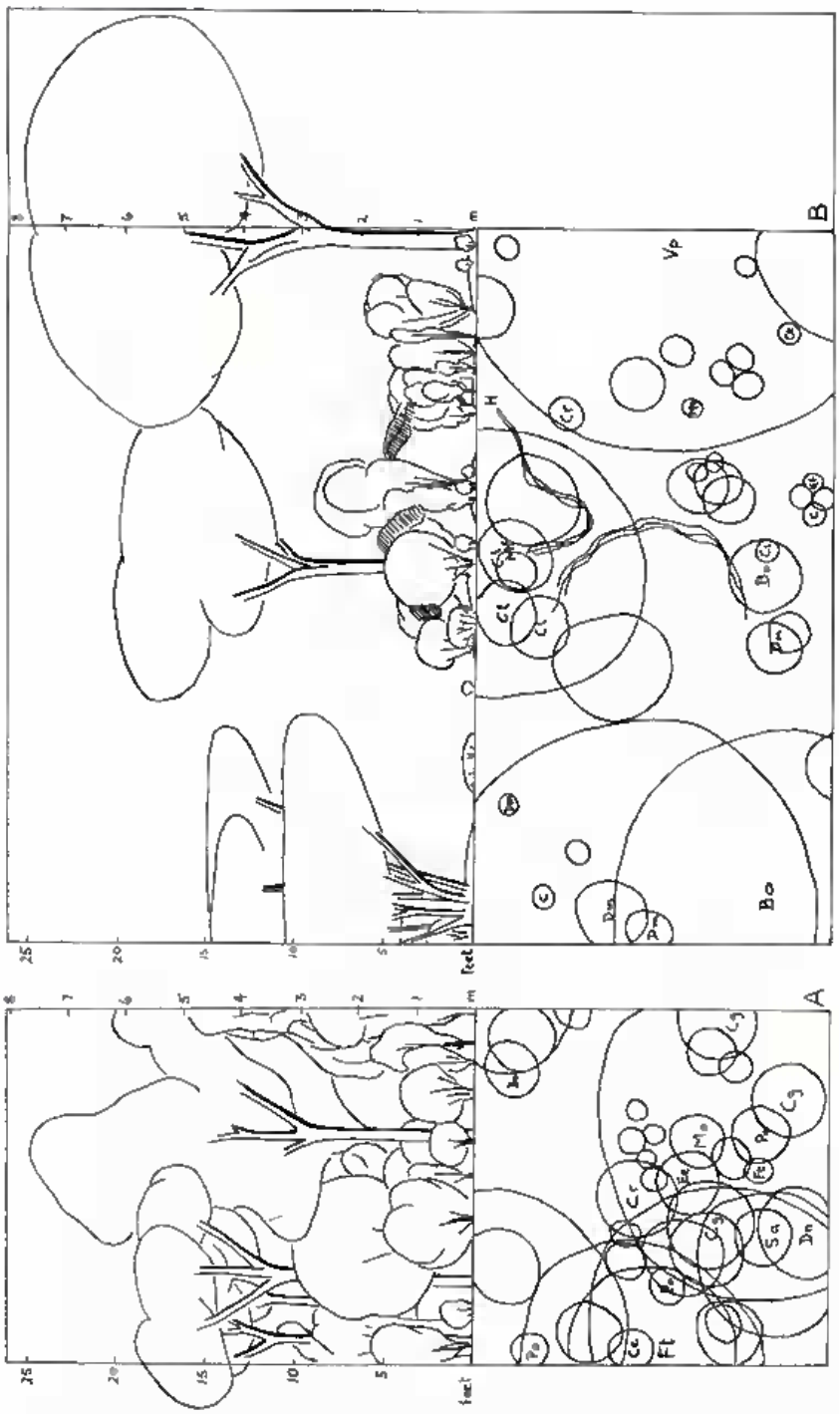


Fig. 3. — **A** : A profile diagram and ground plan of Karroo Thicket, approximately 15 km. North of Ngoma. — **B** : A profile diagram and ground plan of Karroo Savanna Woodland, some 12 km. North of Ngoma.

phragma forest persists as a thicket community, extending down over the slopes of Karroo Sandstone soils until they merge into the contact soils below. Again the trees of the thicket are interlaced with lianes, among which the same species of *Hippocratea*, *Byrsocarpus*, *Dalbergia* and *Strychnos* are prominent, and small trees or large shrubs like *Maerua Friesii*, *Cassipourea congoensis*, *Euphorbia espinosa*, *Fagara triphylla* and *Premna senensis* are characteristic of this Karroo thicket as they are of the understorey of the *Entandrophragma* forest. Also again the same network of game paths formed by buffalo and elephant crisscross the Karroo thicket, maintaining a fairly open structure below the more or less closed canopy at about five or six metres, as can be seen from the transect illustrated in fig. 3 A.

Towards its lower limits, Karroo Thicket has become much degraded. On its southern edge it has been broken down to shrub savanna in a series of fire holes which separate the Karroo Thicket from the Teak Thicket of the Kalahari Sand. To the north the Karroo Thicket is first penetrated by patches of savanna, then entirely gives way to a savanna community.

3. *Karroo Savanna Woodland.*

On Karroo and some contact soils when, as just described Karroo Thicket becomes opened up, a savanna woodland develops having the general appearance illustrated in fig. 3 B. As might be expected, the woody

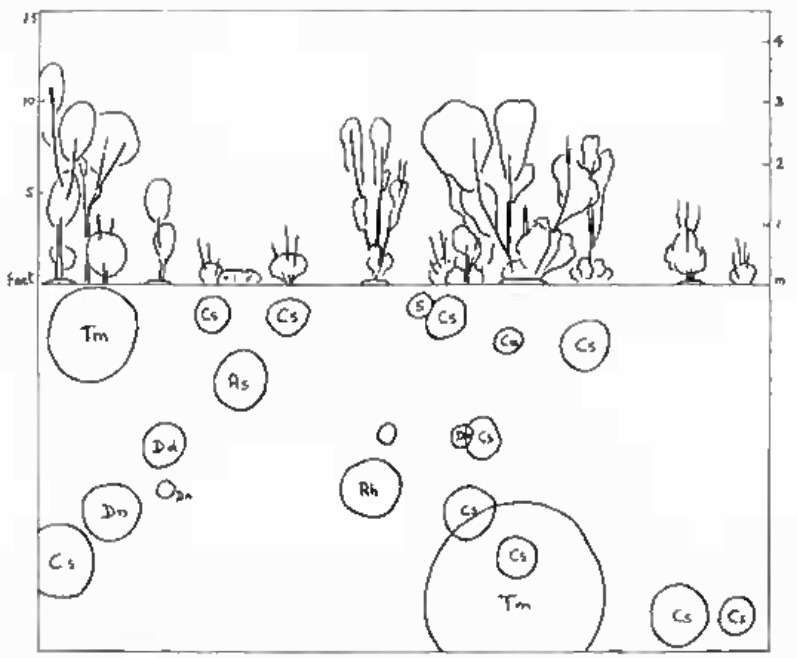


Fig. 4. — A profile diagram and ground plan of Karroo Shrub Savanna, about 12 km. North of Ngoma. Note that many of the smaller shrubs are growing away again after a grass fire some three months previous had burnt them to the ground.

species of this savanna are entirely different from the thicket or forest on Karroo sandstone. *Pericopsis (Afromosia) angolensis* in the area being described seems to occur only in this Karroo savanna woodland.

4. *Karroo Shrub Savanna.*

Where, as will be discussed later, fire has penetrated into Karroo Thicket at its lower limits, a shrubby growth of various woody species, either surviving from the original thicket, or like the savanna grasses, invading the burnt area, occurs. In the resultant shrub savanna, which in many cases must continue to suffer frequent late burning, coppice shoots of *Markhamia obtusifolia* are always abundant.

Continued burning of this shrub savanna apparently eliminates all but a few remaining woody species (fig. 4). Shrub savannas with almost virtually only two woody species, *Combretum ghasalense* and *Terminalia mollis*, are characteristic of repeatedly burnt areas on soils derived from Karroo Sandstone and adjacent contact soils.

B. Kalahari Sand and contact soils

1. *Teak Forest.*

As previously noted, no mature stands of teak occur in the area between the Nkala and Musa rivers, but one of two nearby relict patches some five km. from the right bank of the Nkala river and ten km from Ngoma was examined; a profile and ground plan are illustrated in fig. 5.

Structurally this type of forest is very similar to the *Entandrophragma* forest, with scattered teak emergents rising from 20 to 25 m., above an understorey forming a continuous canopy at 7 to 10 m. This understorey is, however, less dense, and not so obviously parted by game trails. Moreover the presence of *Dichrostachys cinerea* and the scrambling *Acacia schweinfurthiana* in the portion examined suggests that the understorey could be a secondary regrowth colonising abandoned lands once cleared from the forest.

2. *Teak Thicket.*

Teak thickets occur south and east of the Karroo Thickets, but separated from them by the shrub savannas of the "fire-holes" which have eaten into these thickets along what would otherwise be their ecotone.

A number of species such as *Dalbergia Martinii* and *Byrsocarpus africana* are common to both thickets but the Teak thickets which occur principally on Kalahari Sand are characterised not only by the emergence of young teak *(Baikiaea plurijuga)* trees to a height of ten to twelve metres, but by other species of the thicket proper, of which *Popowia obovata* is by far the commonest.

The appearance of Teak Thicket is illustrated in fig. 6. It is even more open below than Karroo Thicket, and the multiple stems of the

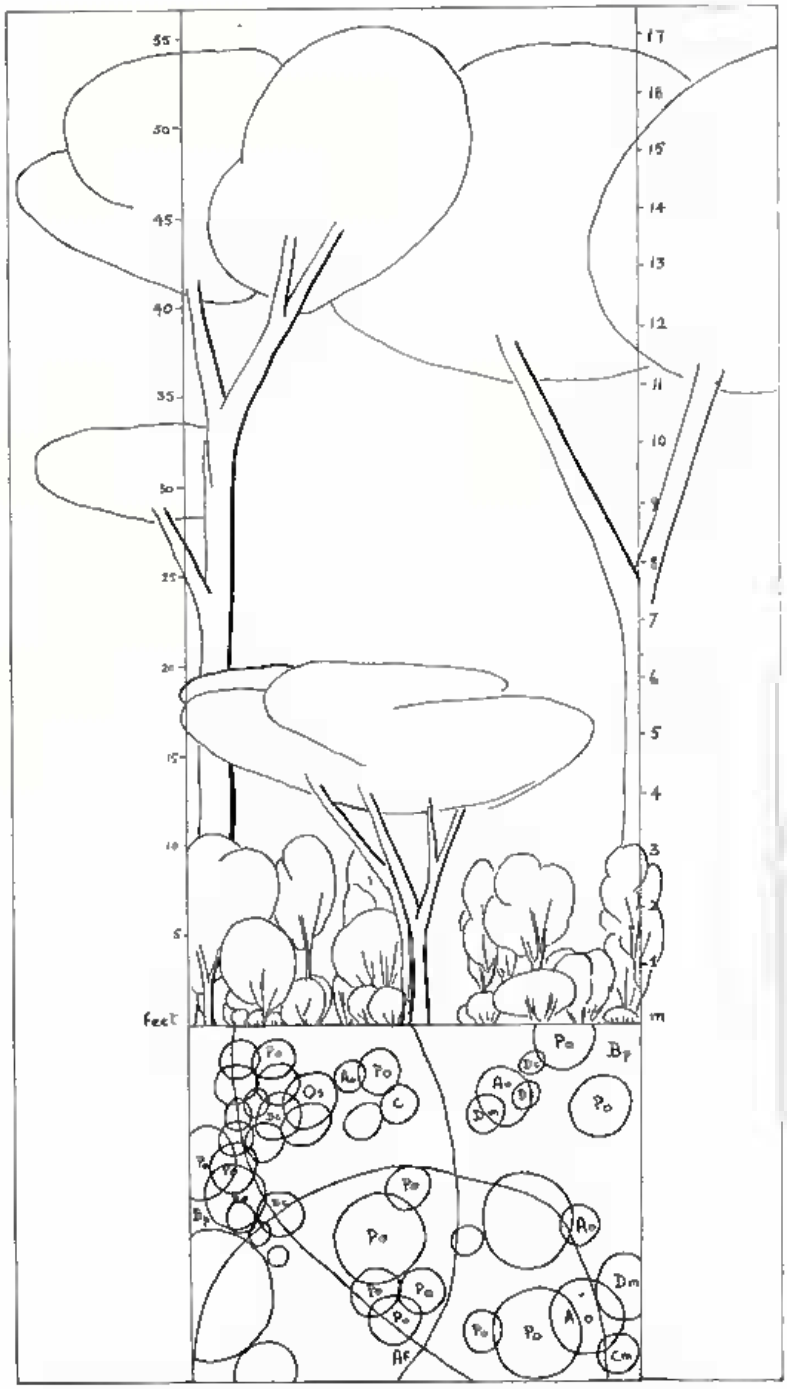


Fig. 5. — A profile diagram and ground plan of Teak Forest, on Kalahari Sand, occurring in a relict patch five kilometres E. of the right bank of the Nkala River.

teak trees suggest that one or more fires may have run through the community at some time.

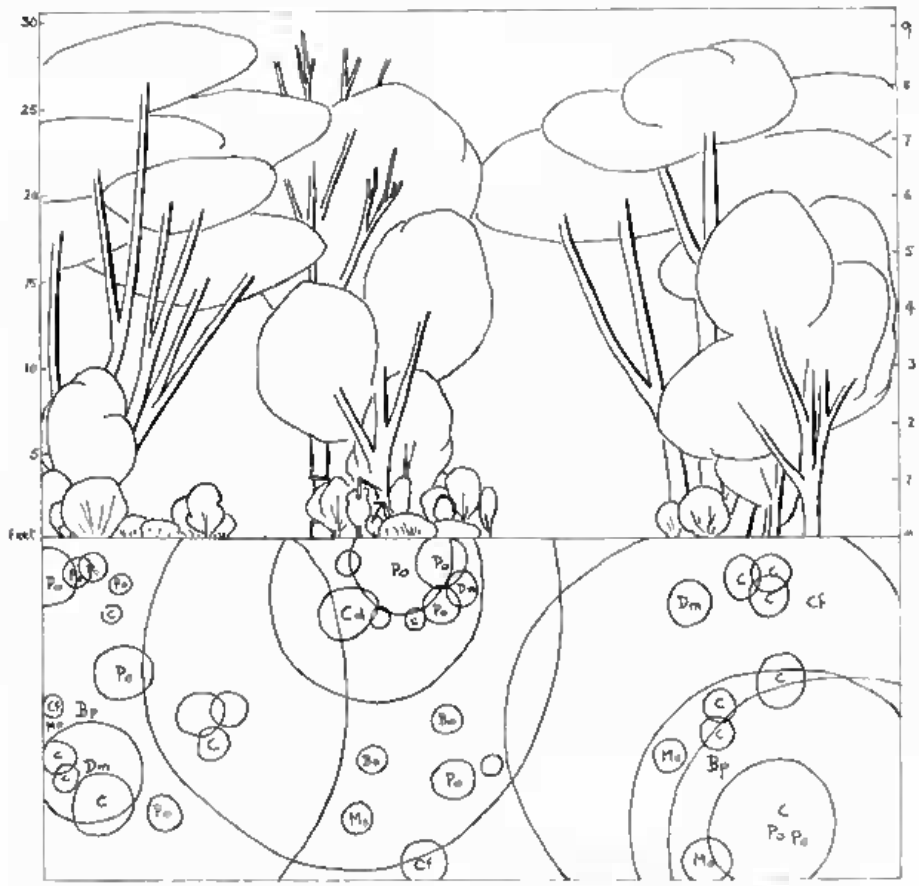


Fig. 6. — A profile diagram and ground plan of Teak Thicket, on Kalahari Sand, about two kilometres South of Vaughan's Loop. Note dead tree ring barked by elephants.

3. *Kalahari Sand Savanna Woodland.*

On Kalahari Sand a savanna woodland very similar in structure and composition (fig. 7) to that on Karroo Sandstone develops under similar circumstances. The most obvious difference between these two communities is the conspicuous presence on the Karroo Sandstone and contact soils of the tree *Pericopsis angolensis.*

4. *Kalahari Sand Tree Savanna.*

Communities of this type appear following the clearing for cultivation purposes of the thickets which as will be seen later develop on land already cleared at least once previously. Tree Savanna was only found on Kalahari Sand, and the trees present, which had been allowed to survive from the otherwise cleared thicket, were sometimes species like teak or *Ricinodendron Raulanenii*, present in the original undisturbed

vegetation, sometimes *Terminalia sericea* and other species, coming in with the pioneer secondary communities (fig. 8).

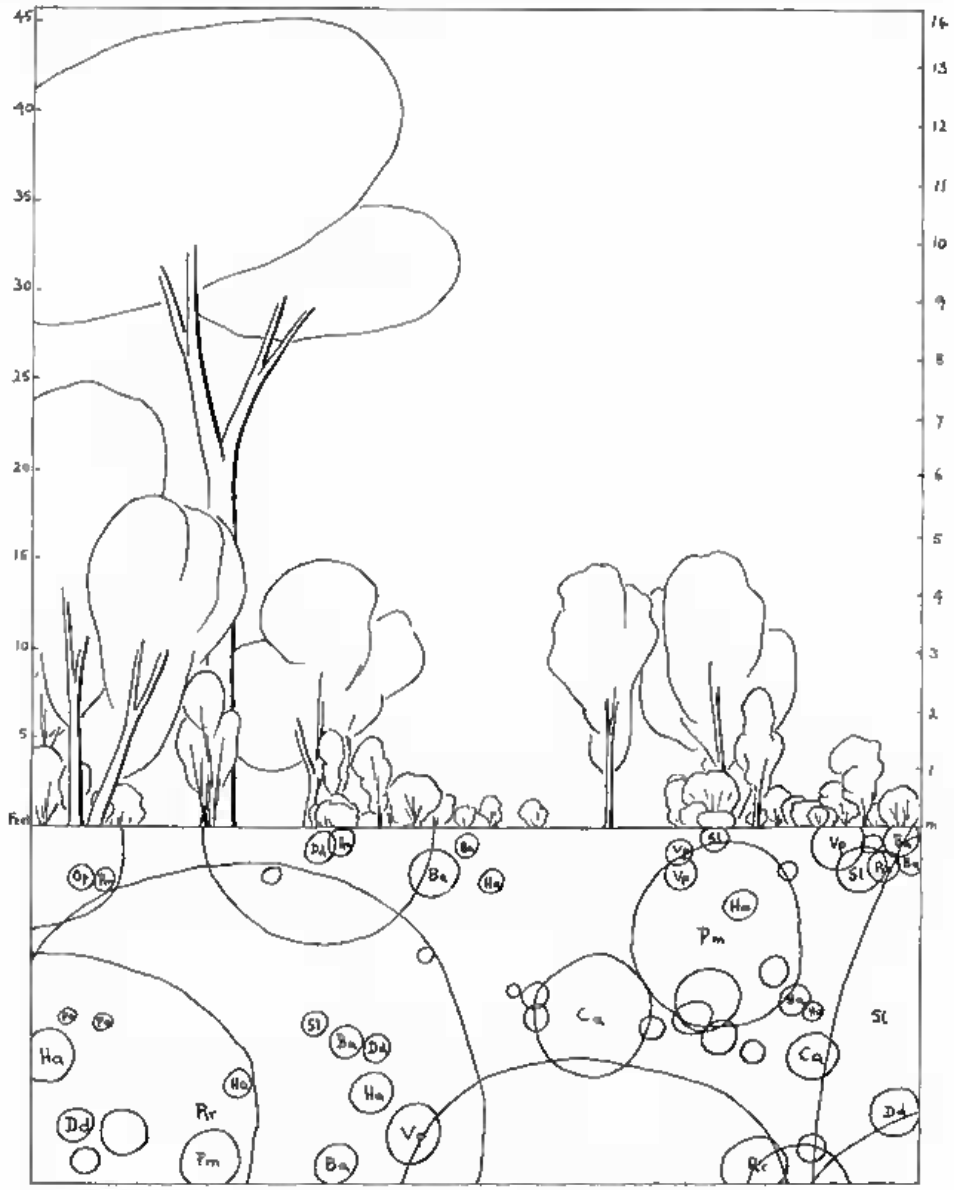


Fig. 7. — A profile diagram and ground plan of Kalahari Sand Savanna Woodland, about three kilometres North of Ngoma.

5. *Kalahari Shrub Savanna.*

Shrub savannas on Kalahari Sand are not very different in structure or composition from those derived in a similar manner on Karroo and contact soils (fig. 9 A).

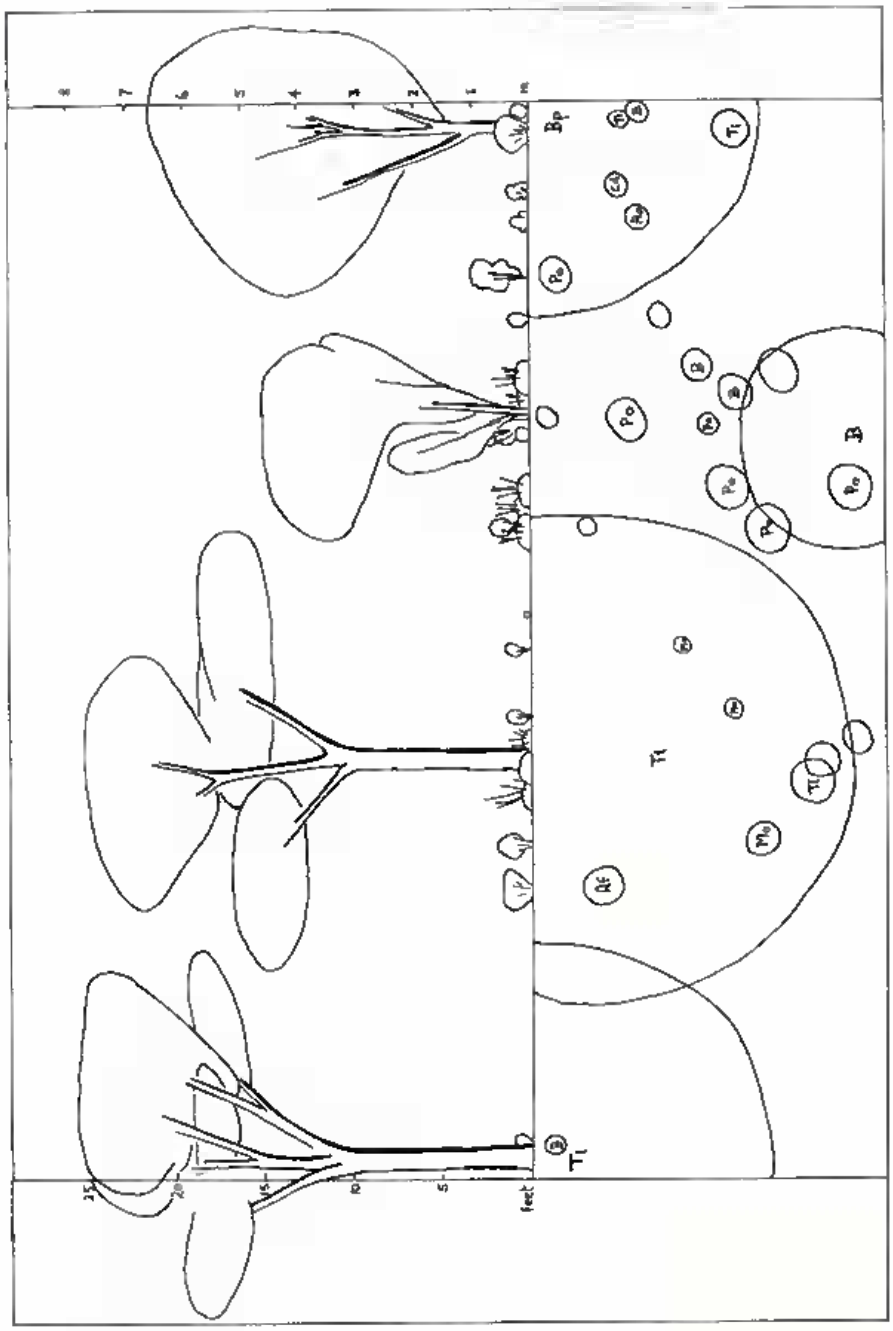


Fig. 8. — A profile diagram and ground plan of Kalahari Sand Tree Savanna, with mature trees of *Terminalia sericea* and young teak: about two kilometres South of Vaughan's Loop.

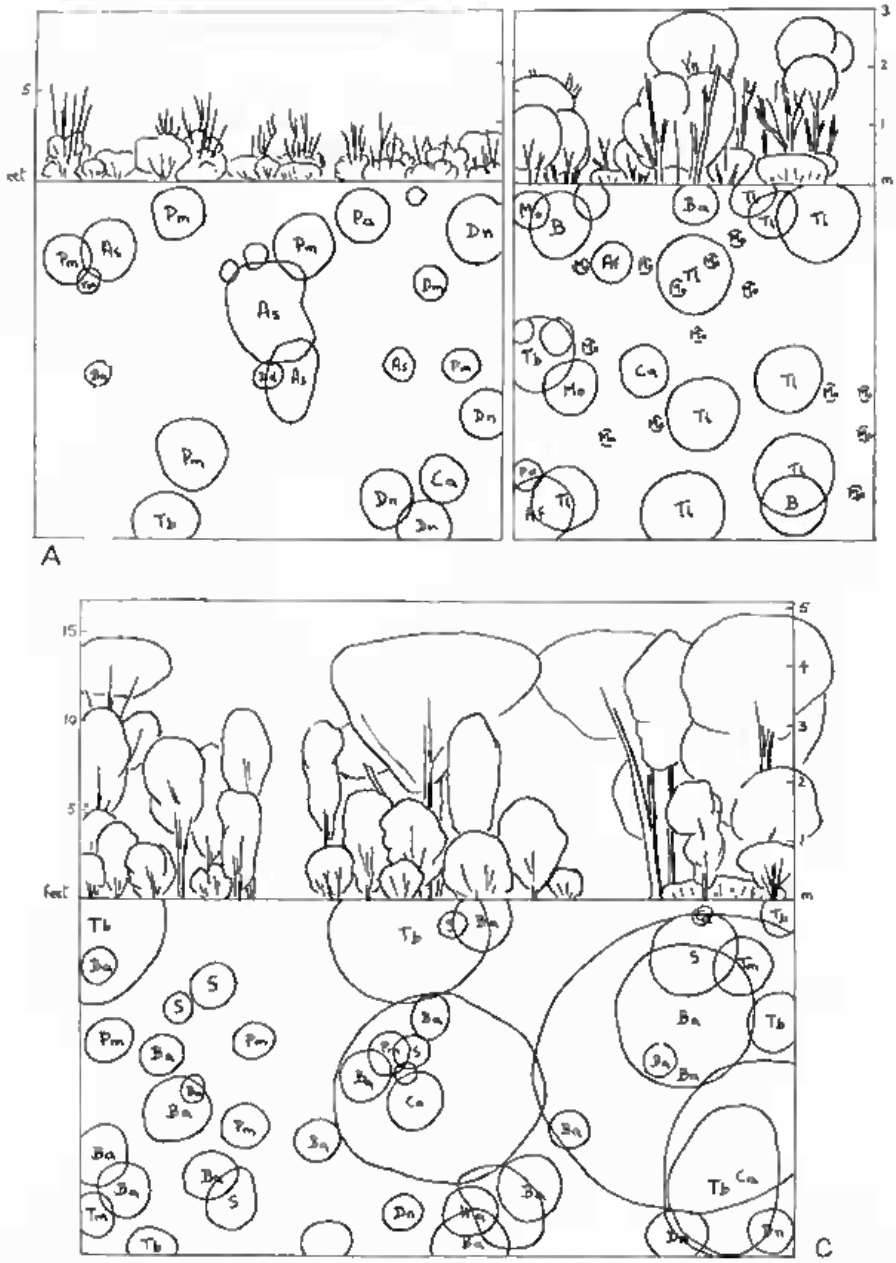


Fig. 9. — **A :** A profile diagram and ground plan of Kalahari Shrub Savanna : adjacent to transect in fig. 8. Nota regrowth after grass fire some three months previous. — **B :** A profile diagram and ground plan of a young *Terminalia* Thicket on Kalahari Sand. Nota the frequent occurrence of small shoots of *Markhamia obtusifolia* between the *Terminalia* clumps, which have been burnt between one and two years previously. Near transect in fig. 6. — **C :** A profile diagram and ground plan of a fairly old *Terminalia* Thicket on Kalahari Sand , about two kilometres North of Ngoma. No signs of any recent burning.

6. *Terminalia Thicket.*

This community was found exclusively on Kalahari Sand, and appears invariably to represent a pioneer stage in the recolonisation of old lands. Two different aged *Terminalia* thickets are illustrated in figs 9 B and 9 C.

The dominant species in some instances is recognisably some form of *Terminalia sericea* agg. This species, however, is not readily distinguished in its vegetative condition from *T. kaiseriana*, *T. sessiliflora*, *T. silozensis*, *T. erici-rosenii*, and in any case there is almost certainly bybridisation between some or all of the species.

Terminalia thicket, because it develops directly from abandoned lands, tends to occur in small scattered patches and appears little favoured by visits from the larger mammals, perhaps because the shelter it provides is too scanty.

7. *Thorn Thicket.*

This type of vegetation differs from *Terminalia* thicket only in that it is dominated by a thorny species, either *Acacia Fleckii* (fig. 10 A),

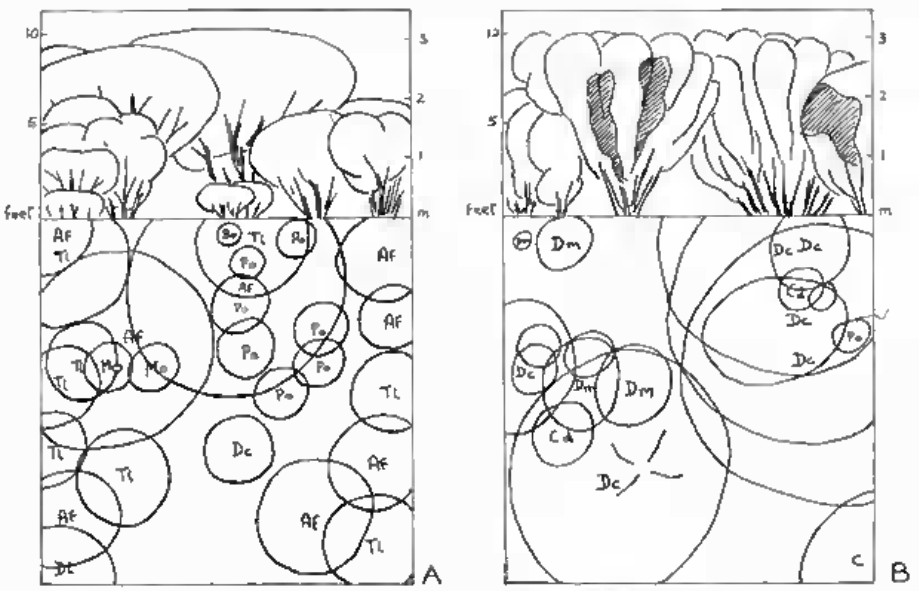


Fig. 10. — **A :** A profile diagram and ground plan of *Acacia* Thorn Thicket, near site of transect of fig. 8. **B :** — A profile diagram and ground plan of *Dichrostachys* Thorn Thicket, near site of transect of fig. 8.

or *Dichrostachys cinerea* (fig. 10 B), but although having a similar ecological status it occurs in more continuous areas. As with the first two thicket types, while it forms a continuous canopy above, it is kept very open for several metres from the ground by bulfalo and elephant penetration.

CONCLUSIONS

It is possible to arrange the thicket communities described here in a tentative succession scheme illustrating their ecological status and their relation to the other communities of the area. There appear to be two main successions, the one on Kalahari Sand, illustrated in fig. 11, the other on soils derived from Karroo sandstone and on contact soils (fig. 12).

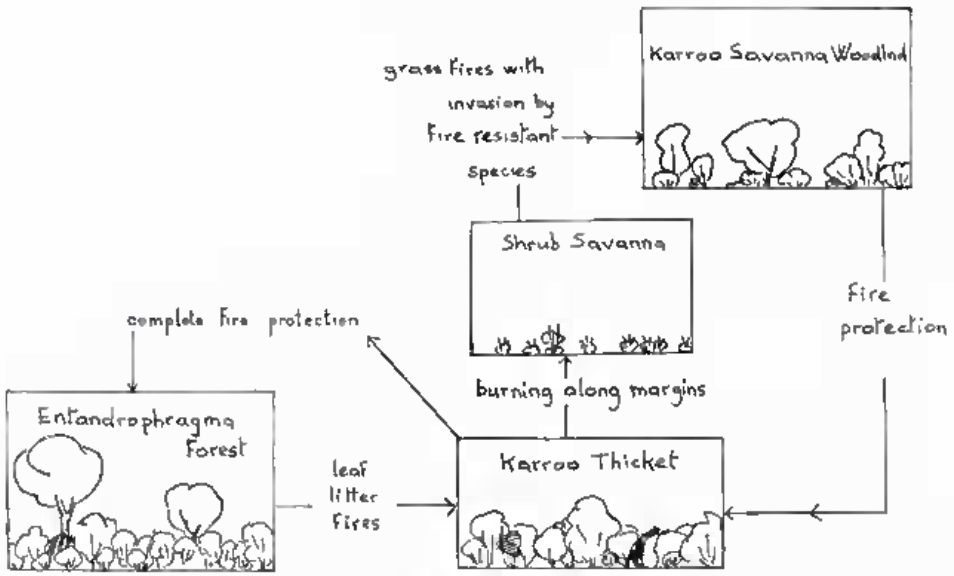


Fig. 11. — Schematic representation of suggested relationships between the various communities described on Karroo Sandstone soils, and the principal ecological factors which are responsible for the replacement of particular communities by others.

It seems that in both successions thickets represent only seral stages leading, in the absence of further disturbance, to dry deciduous forest communities, dominated in the one case by *Entandrophragma caudatum*, in the other by *Baikiaea plurijuga*, a variant of the latter on shallow Kalahari Sands having *Brachystegia spiciformis* as dominant.

Thicket communities, it would appear, can develop in either of two ways. In the one instance they arise because both *Entandrophragma caudatum* and *Baikiaea plurijuga* are extremely fire susceptible. Litter fires running through forests with either as dominant will remove all specimens of these two species. Whereas following a litter fire, most of the forest understorey species will soon regenerate from coppice shoots, giving rise to thicket communities, the teak and the *Entandrophragma* are only re-established by the germination of seed.

In the second of the processes by which thicket can arise, thicket forming species invade the pioneer communities which develop on abandoned lands. It seems that when there is a wild animal grazing factor operating at high intensity, that is, more particularly where buffalo

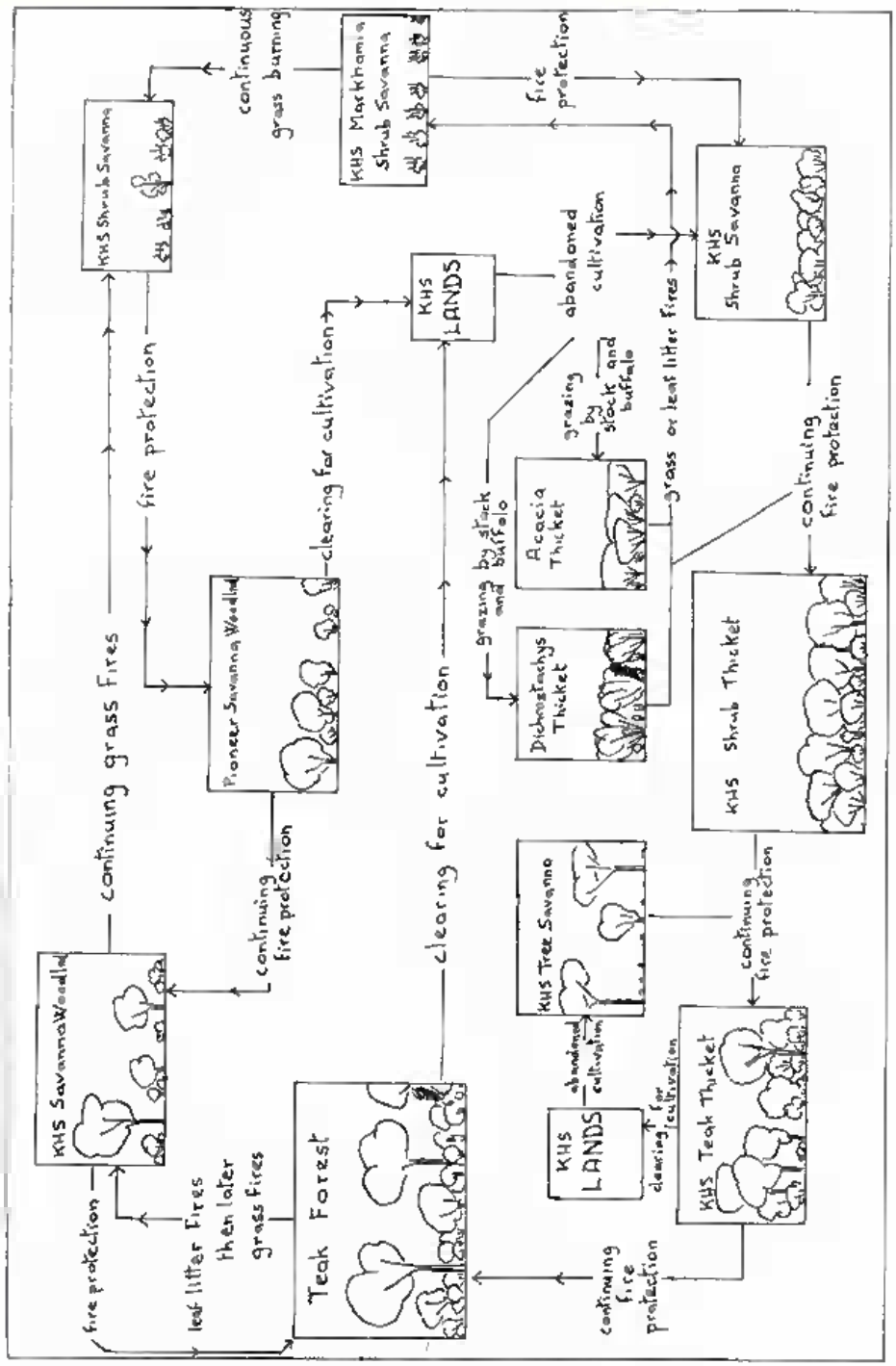


Fig. 12. — Schematic representetion of suggested relationships between the various communities described on Kalahari Sand soils, and the principal ecological factors which are responsible for the replacement of particular communities by others.

herds are frequent visitors, the seedlings of *armed* thicket species tend to predominate in such pioneer communities. This must be the explanation, perhaps associated with grazing by domestic stock also, for the origin of the thorny thicket variants dominated by *Acacia Fleckii* or *Dichrostachys cinerea*.

In the absence of cultivation clearings, thicket is not readily attacked by fire. Only two shade-specialised grasses are present, mostly as scattered individual plants. Grazing animals may in any case remove such grasses before they constitute a small fire hazard, and the larger game species, like buffalo and elephant, maintain at a minimum by trampling the amount of flammable material within several feet of the ground. Fires in these thicket types in fact must, as in the forests, be spread mainly through the leaf litter on the ground, which will dry out and become combustible when the thicket species are leafless in July, August and September; such litter fires will flare up locally whenever they reach any dead material which has survived the depredations of termites.

From the management point of view, Karroo Thicket in this area will be very easy to preserve, protected as it is upwind by the Teak Thickets of the lower ground. Occasional fires will only create temporary fire-holes which the thicket will rapidly recolonise. Complete exclusion of fires can be expected to result in the slow spread of *Enlandrophragma* and the recreation of dry deciduous forest in place of thicket. As the *Enlandrophragma* forest understorey is very similar to Karroo thicket, this succession would not be expected to have any significant effect on the attractiveness of this community to the various game animals which presently use it.

The teak thickets, being on lower ground and more in contact with areas of grass savanna, are more exposed to the hazard of chance fires. Fire-holes will have to be effectively protected from further fire damage. Moreover even though the teak thicket may regenerate quickly after a fire, teak itself will be eliminated for a much longer period, presumably until seed buried in the soil has germinated and the seedlings become established. Complete fire protection of the teak thickets may be expected to result in the ultimate recreation of teak forest. In this case also, the understorey of the forest appears not to differ significantly from the thicket communities, at least as far as occupation by the major game animals are concerned.

The Thorny thickets and *Terminalia* thickets would appear almost impossible to maintain, unless an indigenous human population practicing traditional methods of agriculture is re-introduced into the area. These two plant communities are pioneer stages in the re-colonisation of cleared land on Kalahari Sands and contact soils, and do not appear to be present alternatively in areas devastated by fire, or even to reform themselves when burnt.

DISCUSSION

The idea that thicket communities represent the remains of a dry deciduous forest understorey is by no means new. Thus KEAY (1949) postulated that the "mutemwa" vegetation of N. Rhodesia once existed also in the Sudan Zone of Nigeria, with a thick understorey of erect and scandent shrubs, before fires destroyed the understorey species, which were later replaced by savanna grasses to form what is now called woodland and savanna. Rather similar suggestions have recently been developed by CLAYTON (1961) in respect of "transitional woodland" in Nigeria. AUBRÉVILLE (1956) in defining dry deciduous forest in Africa states that it is characterised by a dense thicket undergrowth, and that woodlands are probably derived forms of dry deciduous forest. Similarly FANSHAWE (1956) considers that in Northern Rhodesia "Miombo woodland" carries an understorey of ever-green thicket in the higher rainfall areas and deciduous thicket with a lower rainfall.

It does indeed appear that the thicket communities described here represent the last vestiges of dry deciduous forest types of vegetation, local examples of a great assemblage which once covered most of Africa between the Moist Forests and the desert steppes. It seems unlikely that the fact of the survival of these relict communities here in this area of the Kafue National Park can be dissociated from the visible concentrations of large game animals, and more particularly of buffalo. MITCHELL (1961) has already postulated that the presence of herds of these and other game mammals has until modern times protected the teak *(Baikiaea plurijuga)* forests of Southern Africa from fire, and so from degradation to a woodland form.

The vegetation of the area studied can therefore be envisaged as originally forming a dry deciduous forest, stretching continuously right to the edaphic grasslands of the river flood-plains. The emergent tree dominants would vary with the catena pattern, as would the representation of the small trees and lianes forming the understorey. There would be then, as today, no termite mounds within the forest area, although termitaria would be, then as now, common and widely distributed. Many game animals would graze and browse in the forest understoreys, finding a substantial proportion of their food in the fruits and seeds of understorey species, many of which like *Popowia obovata*, *Strychnos* (White sp. 2) and *Grewia flavescens* are known to be edible.

Fires started by lightening in the grasslands of the dambos would only occasionally penetrate these forests, never repeatedly in the same place, so that regeneration would always be both possible and rapid. Such regeneration following an accidental burn can still occasionally be seen.

With the arrival on the scene of agricultural populations settling on the outer margins of the flood plains, the situation would change radically. Deliberate firing of the dambo grasslands would be an annual

event, and the adjoining forest margins would likewise be burned annually. First the adjacent forest would lose its fire-susceptible dominants, and be reduced to thicket. Then the thicket itself would be broken up and opened out to savanna-woodlands and tree savannas by the loss of the less fire-resistant species. Meanwhile sheet erosion of the exposed soil would increasingly occur, and especially between the termitaria, whose soil was sheltered by a tree cover from the erosive action of fast-falling rain-drops. Gradually because of this erosion, the termite mounds, representing the original land surface, would appear to rise higher and higher above the surrounding eroding land.

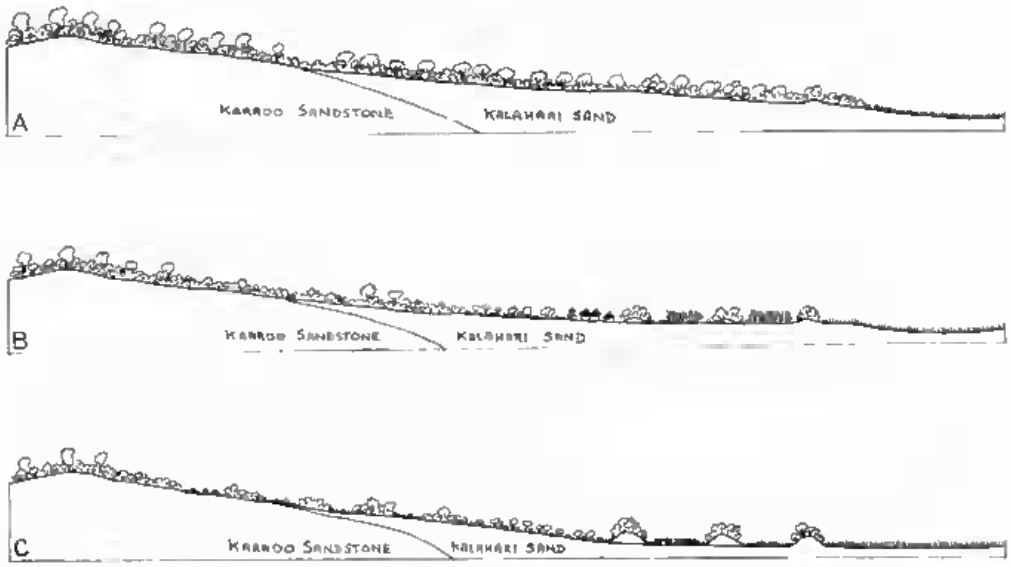
So around the stream-head dambos leading up to the watershed, the edaphic grasslands would pass on their margins into derived grasslands established on a lowered land surface, ever eroding between the termite mounds and maintained by fire as grassland, or at most as shrub savanna of the most fire-resistant woody species.

Clearing of the forest adjoining the dambos to create cultivated lands would complicate and accelerate this ecological degradation.

On the Kalahari Sands the forests gave way to the familiar pattern of a *Brachystegia-Julbernardia* woodland of fire resistant trees, leading down through a tree savanna where the woody growth is clumped on huge termite mounds, to an extended dambo grassland. On Karroo Sandstone and contact soils, mostly on higher ground away from water, and thus largely undamaged by cultivation clearings, the increased incidence of fires following human occupation of the areas first removed the fire-susceptible forest dominants from all but the deepest heart of the forest on the ridges. Then through extensive development of regenerating shrub savannas on the lower ground more exposed to fire, the one-time forest margins suffered sheet erosion, with the same survival of high termite mounds, topped by woody growth, and a shrub savanna of highly fire-resistant species between.

These changes in the vegetation on Karroo Sandstone and contact soils, and on Kalahari Sand, are represented schematically in fig. 13.

Whether the vegetation of present day termite mounds represents the original vegetation cover in whole or in part cannot be considered here as this was ignored in the present investigation. Although frequent reference is made to termite mound vegetation in ecological work in tropical Africa, and this has even been the subject of special study in this area (Wild, 1952), there does not appear previously to have been any suggestion that the mounds have been created by the erosion of soil between them, as well as by their emerging above the surrounding land by the addition of material from below and by the accumulation of material crumbling from successive termitaria. Such a new explanation (Boughey, 1963) appears to have much to commend it. Termite mounds are but rarely found in areas which have for long been under undisturbed Moist Forest; nor do they appear in the driest areas of savanna woodland (where sheet erosion is not a significant factor). They are in fact characteristic of just those areas and sites which might



be expected once to have been covered by dry deciduous forest, but now carry only woodland, or degraded savanna vegetation. They are most characteristic of those sections of the catena patterns adjoining the edaphic grasslands of the flood plains, where fires have been most frequent, and run-off and consequently sheet erosion at a maximum.

Références

Aubréville, A. (1949). — Climats, Forêts et Désertification de l'Afrique Tropicale. Paris.

Aubréville, A. (1956). — Definitions physionomiques, structurales et écologiques des forêts claires en Afrique. C.S.A. publ. n° 52 : 81-7.

Boughey, A.S. (1963). — A possible course of evolution of termite mounds in Central Africa. Proc. Centr. Afr. Sci. et Med. Congr. (inpress).

Clayton W. D. (1916). — Derived savanna in Kabba Province. Nigeria. J. Ecol. **49** : 595-604.

C.S.A. (1956). — C.S.A. publ. n° 26.

Fanshawe, D. B. (1956). — Floristic composition of Miombe Woodland. C.S.A. publ. no. 52 : 55-7.

Hopkins, B. (1957). — Pattern in the plant community. J. Ecol. **45** : 451-63.

Keay, R. W. J. (1949). — An outline of Nigerian Vegetation. Lagos.

Lebrun, J. & Gilbert, G. (1954). — Une Classification écologique des forêts du Congo. I.N.E.A.C., Ser. Sci. n°. 63.

Mitchell, B. L. (1961). — Ecological aspects of game control measures in Africa. Kirkia, **1** : 120-28.

Richards, P. W. (1952). — The Tropical Rain Forest. Cambridge.

Ross, R. (1954). — Ecological studies on the rain forest of Southern Nigeria **IIt** Secondary succession in the Shasha Forest Reserve. J. Ecol. **42** : 259-82.

Taylor, C. J. (1960). — Synecology and Silviculture in Ghana. Edinburgh.

Trapnell, C. G. (1943). — Soils, Vegetation and Agriculture of North-Eastern Rhodesia. Lusaka.

Trapnell C. G. and Clothier (1937). — The soils, vegetation and agricultural systems of North-Western Rhodesia. Lusaka.

White, F. (1962). — Forest Flora of Northern Rhodesia. Oxford.
Wild, H. (1952). — The vegetation of Southern Rhodesia termitaria. Rhod. agric. J. **49** : 280-296.

ABSTRACT

The occurence of several thicket types in the Kafue National Park of Northern Rhodesia is recorded. The structure of these thickets and that of other climax and seral communities in the area is described and illustrated.

Two hypothetical ecological successions are outlined, the one on soils derived from Karroo Sandstone, the other on Kalahari Sand, and the several thicket types referred to their positions in these schemes.

The present vegetation of this area is related to hypothetical dry deciduous forest communities which have now largely disappeared, supposedly with the advent of agricultural man.